# The Role of Earthworms in Soil Formation

**Jan Frouz**

**Abstract** Despite being an important ecosystem engineer, earthworms cannot form soil alone. The role of earthworms in soil formation occurs through interactions with other soil-forming factors namely parent material, climate, topography, vegetation, and time. I begin by exploring questions about how earthworms interact with these soil-forming factors, namely, which of these affect earthworm activity and how earthworm activities can modify how these factors contribute to soil formation. Then, I examine how earthworms are involved in soil formation at various spatiotemporal scales. Earthworms form biostructures with dimensions of several millimeters (feces) to 1 to several meters (burrows); however, these biostructures affect soil processes that occur at smaller spatiotemporal scales as well as hydrologic and vegetative processes at much larger scales. Since earthworm biostructures persist in soil, they can have an impact on soil processes beyond the lifespan of an earthworm. I conclude with an analysis of the extent of earthworms and soil formation across spatiotemporal scales.

## 1 Introduction

Earthworms have a tremendous role in soil properties across spatiotemporal scales. In this chapter, I focus on the effect of earthworms on soil formation. I will approach this question from two different views. In the first part of the chapter, I will explore how earthworms interact with key soil-forming factors. How soil-forming factors, namely, geological substrate, climate, topography, biota, and time of soil development may affect earthworms and how earthworms can modify the effect of these soil-forming factors. In the second part of the chapter, we will explore how

J. Frouz (✉)
Biology Centre CAS, Institute of Soil Biology and Biogeochemistry, České Budějovice, Czech Republic

Charles University, Prague, Czech Republic
e-mail: frouz@natur.cuni.cz

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earthworms affect processes of soil formation from soil aggregates to soil profile and beyond.

## 2 Earthworm Interacting with Soil-Forming Factors

Soil formation is a process during which mineral material interacts with organic matter under the influence of soil-forming factors to produce new soil materials. Soil-forming factors are parent material, which provides the mineral constituents of the soil, which together with climate, topography, and biota determine the speed and magnitude of soil formation during a period of time (Weil and Brady 2016). In this chapter, I will explore how these soil-forming factors may interact with the soil-forming activity of earthworms, which have engineering capacity. It is also interesting to understand how earthworm activity can be affected by soil formation, which may make the soil profile a more or less habitable environment for earthworms.

### *2.1 Parent Material*

Parent material is the unconsolidated weathered rock that may be transported and deposited, e.g., due to water or wind erosion or glaciers and/or other forces (Weil and Brady 2016). Both character of rock and transformation processes determine the properties of the parent material (due to the character of weathering, leaching, mixing, etc.). The proportions of clay and other particles (sand, silt) in a given mass of soil determine its texture, also the chemical properties of the parent material determine the availability of nutrients and pH. Earthworm presence has also been shown to be closely related to the geological history of the area especially glaciation (Mathieu and Jonathan Davies 2014; Rutgers et al. 2016), but links to particular bedrock are less established. Moreover, also due to the fact that soil can form either directly from bedrock or from saprolite (which is in situ weathered bedrock), but also from rhyolite (which is clastic, partly weathered material, various sources, local, as well as those brought on the place by various transport processes). The fact that weathered material from which soil in originating may not be produced locally, but transported here from various sources, made link between bedrock, soil properties and earthworms more complex. Furthermore, in some soils such as organic peat and fen soil, the effect of mineral is less pronounced, and thus texture is not predictive of earthworms and their activity.

Still, earthworm communities are strongly dependent on soil texture and pH (Hendrix et al. 1992; De Wandeler et al. 2016), which are directly or indirectly dependent on the parent material. Earthworms tend to preffer loamy soil and close to neutral pH. Also, the effect of soil fauna and earthworms in particular on soil properties strongly depends on substrate texture and pH (Józefowska et al. 2017).

Finally, various bedrock types can produce soils with similar pH and texture, which makes the relationship between bedrock and earthworms even less tight.

The weathering of parent material is affected by the presence of earthworms. For example, by creating preferential flow pathways, earthworms accelerate water infiltration from the soil surface to the subsoil and in the soil bedrock interface, which can indirectly affect weathering. Direct weathering of clastic minerals by earthworms is well-known, based on reports dating back Darwin (1881), who describes that the red color of red-oxide sand disappeared after passing through earthworm intestines. There are some studies that explore the effect of earthworms on clay minerals using X-ray diffraction (Hušák et al. 2005; Carpenter et al. 2007). These rather preliminary studies report earthworms increase the weathering of anorthite, biotite, smectite, and kaolinite. These results also suggest the transformation of smectite to illite and the formation of a new mineral phase from kaolinite. Similarly Pop (1998) found that *Octodrilus* earthworms affect the clay mineralogy and formation of illite in the soil. However, the mechanisms behind these changes are not quite clear. Earthworms accelerate basalt weathering and increase the availability of potassium and phosphorus from minerals bearing these elements (Mackay et al. 1983; Liu et al. 2011), suggesting earthworms may speed up the chemical weathering of these minerals. On the contrary, earthworms may reduce metal mobility in the soil in certain circumstances (Sizmur and Hodson 2009). The effect of earthworms on mineral weathering and hence nutrient availability in soil may be ecologically significant; unfortunately, the effect of earthworms on minerals and rock weathering is highly underexplored.

## *2.2 Climate*

Climate is a key soil-forming factor. Climate affects earthworm distribution (Phillips et al. 2019; Fourcade and Vercauteren 2022) and consequently their function in the ecosystem. This is the consequence of the geographic distribution of earthworms, along with the temporal variation in earthworm activity and population dynamics in response to ongoing climate change (Singh et al. 2019; Phillips et al. 2019; Fourcade and Vercauteren 2022). Earthworms are unlikely to modify local soil thermal conditions but may modify the moisture factor of climate that influences soil formation. For example, one of the most important effects of climate on soil formation is the degree to which water percolates through the soil profile, as this alters clay movement in the soil profile and triggers the soil-forming processes associated with eluviation and illimerization. Earthworms may affect these processes by the creation of preferential flows, which affect water movement in soil profile or by upward movement of clays due to bioturbation (Sauzet et al. 2023). For example, Jačka et al. (2021) indicate that infiltration (K) was about threefold higher in alder plantation, densely colonized by earthworms, compared to neighboring spruce where earthworms were almost absent.

## 2.3 Topography

Topography is another important soil-forming factor. Topography causes variation in environmental conditions and hence also conditions for soil formation but perhaps more importantly topography triggers many transport processes, such as landslides, erosion, and solifluction that cause soil-forming materials to be transported from one habitat to another. Already Darwin (1881) pointed out that earthworms may affect these processes by depositing casts on the soil surface that subsequently become susceptible to erosion. Also, other studies show that casts or droppings produced by soil fauna may be subject to more erosion than the surrounding soil matrix (Yair 1995; Le Bayon and Binet 2001). However, the interaction of earthworms and erosion may be more complex, as discussed below. For example, earthworms increase infiltration (Ehlers 1975; Francis and Fraser 1998; Jačka et al. 2021), which may potentially reduce surface runoff and water erosion. Eroded material in many cases gets deposited in other places in the landscape. Since Darwin's times (Darwin 1881), it is known that earthworms can bury the objects in the soil. Earthworms may also cause the burial of the sedimented layers and its mixing into the soil underneath.

## 2.4 Biota

Vegetation is the most important soil-forming factor that influences the earthworm community (Mathieu and Jonathan Davies 2014; Rutgers et al. 2016). This is because vegetation provides substrates and habitat for earthworms. The effect of vegetation on soil formation is largely mediated by the response of soil biota, particularly earthworms, to the presence of particular plant communities (Frouz et al. 2013a, 2013b; Ponge 2003, 2013; Józefowska et al. 2017; Frouz 2018). The evidence supporting this claim comes from several sources: (1) correlation between certain vegetation traits, earthworm abundance (and/or activity), and soil properties (Frouz et al. 2013a), (2) manipulation experiments (Frouz et al. 2006, 2007a), and (3) from the significant change in soil properties after earthworm invasion into a new area previously devoid of earthworms (Hendrix and Bohlen 2002; Bohlen et al. 2004) or in a location where earthworms were eradicated, e.g., by mining activity (Frouz et al. 2008, 2013b). By changing soil properties, earthworms affect other soil biota and change fungal:bacterial ratio, and composition of the soil food web (Frouz et al. 2013b), which, in turn, may affect other soil processes such as aggregate formation or the quantity of carbon stored in soil. This relationship between vegetation, litter traits, and soil faunal activity can be conveniently described by the concept of humus forms (Ponge 2003, 2013; Frouz 2018).

The formation of humus form is affected by litter quality and also by the properties of the soil-forming substrate determining nutrients, pH, and texture (Fig. 1), which determine the composition of soil biota among them earthworms play a

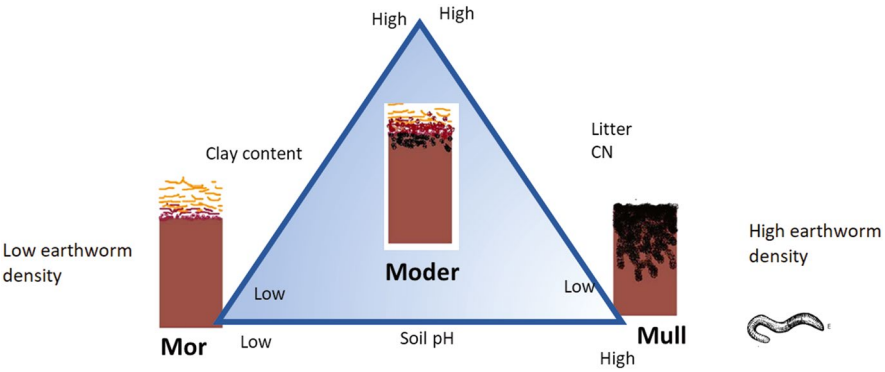


**Fig. 1** Humus forms in undisturbed ecosystems are affected by the soil properties (e.g., clay content, pH) and characteristics of the vegetation, here described as the C:N ratio of the litter layer from senescent leaves and other plant debris

principal role. Soil fauna, namely earthworms, then determine the intensity of bioturbation and the way how bioturbation is performed, which consequently yields in the formation of specific humus form affecting other soil properties that generate a feedback by supporting vegetation with specific leaf traits (Frouz 2018). In soils supplied with litter that has a high C:N ratio and decomposes slowly, namely on substrates that are sandy and acidic, which limit earthworm activity, a mor type of humus develops. The bioturbation effect of fauna in this case is small. Litter is either not eaten by fauna or is consumed by soil mesofauna and transformed into holoorganic mesofauna feces. As a consequence, most litter is decomposed on the soil surface by fungi, leading to a high fungal-to-bacterial ratio (F:B). The activity of soil fauna, namely earthworms, is more pronounced in soil supplied with easily decomposable litter with a low C:N ratio namely in substrates that are close to neutral pH and loamy, resulting in the incorporation of a substantial part of the litter into the soil and in the formation of a mull type of humus (Frouz et al. 2009; Ponge 2003). In a mull humus, macrofauna biomass is high, and there are abundant anecic earthworms that forage for litter on the surface but live deeper in the soil. Bioturbation by macrofauna, and by earthworms in particular, plays a principal role in the formation of the soil profile. Because bacteria dominate in a mull, the F:B ratio is low. Frouz et al. (2013a, 2013b) found that the F:B ratio is more closely related to the intensity of earthworm bioturbation than to the litter C:N ratio. In soils supplied with litter of an intermediate quality, a moder type of humus develops. This type of humus is characterized by an intermediate F:B ratio and an intermediate level of bioturbation that is maintained by litter-feeding macroarthropods (such as millipedes, isopods, and dipteran larvae) and epigeic and endogeic earthworms (Frouz 2018). This basic outline of humus form can be expanded to a more complex classification of humus form (Zanella et al. 2011).

The presence of specific humus forms corresponds with the vegetation and nutrient status of the soil. Also, observations made after the invasion of earthworm-free

sites suggest that earthworm-mediated bioturbation plays an important role in the determination of soil conditions in these sites. For example, Frouz et al. (2009, 2013a, 2013b) reported that changes in macrofauna, namely earthworms' bioturbation activity along a litter C:N gradient, may affect the C sequestration rate in post-mining soils, the F:B ratio, and nutrient availability. This may be due to a feedback in the plant community composition (Frouz et al. 2009). Similar changes in properties of topsoil and vegetation were also observed after earthworm invasion in North American forests, relative to those devoid of earthworms (Hendrix and Bohlen 2002; Bohlen et al. 2004).

Despite the well-documented relationship between humus form and soil properties, there is a weaker relationship between humus from and soil development. While humus form is often the precursor to certain soil types (e.g., mor is often associated with podsols or other spodosol, while mull is related to mollisols, and so on), variable humus form could be associated with the same soil type (Frouz et al. 2013a). There are two reasons for that: first, the formation of a specific soil type is affected by a broader set of soil-forming factors and second, the humus form affects the soil profile close to the surface, specifically the topsoil and overlying organic horizons. These changes can occur quickly and affect processes in deeper soil layers, but it typically takes longer before changes in the deeper layers of the soil profile become visible. More detailed studies are needed to explain how soil fauna activity contributes to the formation of the humus form and evaluate the connection between humus form and particular soil types.

Finally, all soil-forming factors can be important when a sufficiently long timescale is considered. As the time passes and soil develops, its suitability for earthworms will change. Earthworms colonize sites after soil conditions become suitable for their survival, following initial soil development (Frouz et al. 2006, 2007a, 2007b). At the same time, earthworm activity affects the continued soil development in a site-specific manner. For example, Toyota et al. (2013) compared the effect of earthworms on N use efficiency in soils in a tillage–no tillage experiment; soils used in this experiment came from the same field divided into tillage and no-tillage treatment decades ago. In the meantime, earthworms' density increased in no-tillage treatment, which contributed to soil changes. Then earthworms were experimentally removed from both soils and reintroduced in some treatments. Earthworms' presence in tillage soil (with a low-soil fauna legacy) increased N loss by leaching and decreased N use efficiency by plants. In contrast, fauna presence in no-till soil (higher soil fauna legacy) decreased N leaching and increased N use efficiency by plants. Similarly, the effect of earthworms on soil carbon storage changes as the soil accumulates more carbon (Frouz 2017). In soil without any organic matter, the rate of accumulation is slow and increases as organic matter increases, but as the soil approaches saturation, it slows down and eventually stops. More similar examples can be found in Frouz (2024).

## 3 Earthworms and Soil Formation across Spatiotemporal Scales

Earthworms have a direct effect on soil processes that are proportional to their size and lifespan; however, the soil environment maintains traces of earthworm activity, and the cumulative effect of individual earthworms persists across space and time. Consequently, earthworms affect soil processes across spatiotemporal scales. Earthworms produce soil aggregates through their digestive and soil agglomeration activities. The corridors formed by earthworms in the drilosphere allow for gas exchange and the flow of water, dissolved solutes, and particulate transport. The small-scale reactions inside these biostructures can be important at short time scales. Still, the cumulated effects of earthworm-created microstructures contribute to hydrologic and biogeochemical cycling in the whole soil profile, potentially shaping soil formation at the landscape scale.

### *3.1 Drilosphere and Microscale Effect*

Earthworms feed on organic material at the soil surface and inside the soil profile and egest casts (aggregated fecal material) in which organic and mineral particles are mixed (Fig. 2). These feces are deposited either on the soil surface or in cavities inside the soil. Moreover, earthworms move by pushing soil on sides, this creates a layer of compacted soil around earthworm corridors, which can be enriched by earthworm mucus and excrement. Drilosphere differs from the surrounding soil (Frouz et al. 2011). It typically has higher organic matter content than surrounding soil, greater aggregate stability, and elevated microbial activity. Microbial community change as litter and mineral matrix gets mixed into earthworm cast, namely fewer fungi and bacteria prevail (Frouz 2018). Microbial activity changes as well, these changes vary in time, microbial activity may be enhanced in young earthworm casts and suppressed in older ones. Mixing of organic matter in the aggregates can contribute to soil carbon storage as reviewed by Angst et al. (2019, 2022). Earthworms mix small fragments of particulate organic matter (POM) in the mineral matrix inside aggregates. Decomposition of this occluded POM gradually declines without substantial chemical changes (Angst et al. 2017). The reason is that occluding organic matter in clay, which is typically water-saturated, reduces the access of oxygen, which has to move inside by diffusion. Diffusion is a slow process, and part of the oxygen can be consumed by microbes in the surface layer of aggregates, this can yield in anaerobic conditions inside aggregates, which slows down decomposition. Also, the removal of the product of metabolism from occluded organic matter can be reduced by the same mechanism, which further restrains the decomposition of occluded organic matter. Moreover, microbes grow massively in occluded organic matter, namely, in their vicinity, using dissolved organic matter that leaches out of occluded POM. This hotspot of microbial biomass can eventually

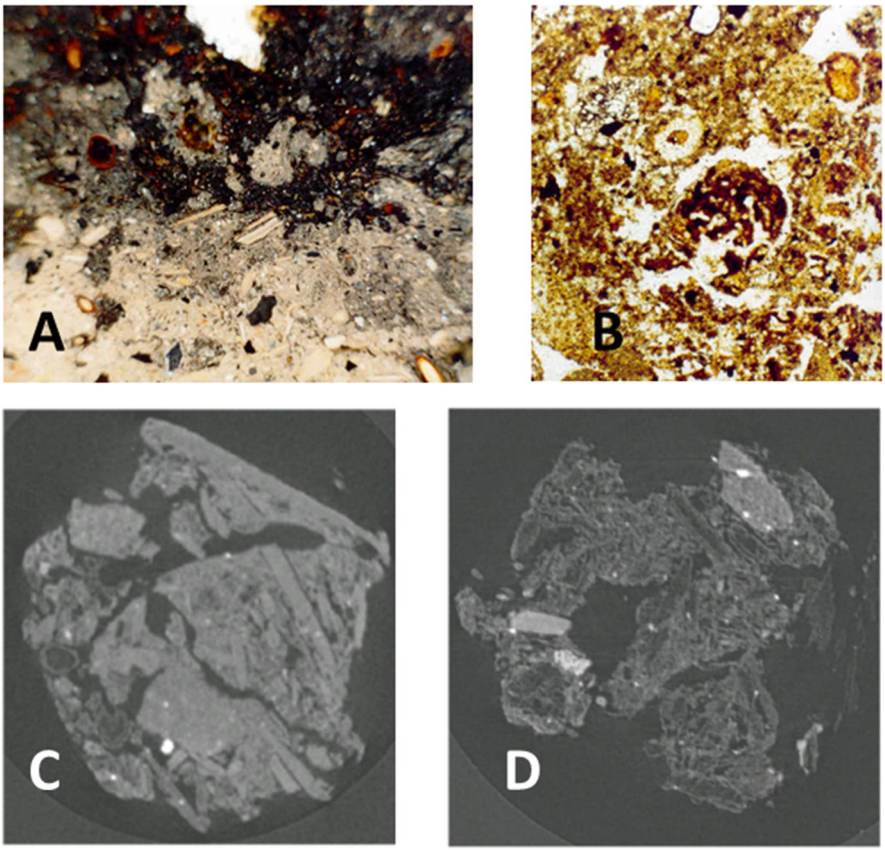


**Fig. 2** Comparison of X-ray of aggregate that was formed without being affected by earthworms (**a**), with earthworm cast (**b**) and view of earthworm cast in the immature soil profile (**c**), and a detailed view of the earthworm cast from the same location (**d**)

turn into microbial necromass following the lysis of microbial cells. The microbial necromass remains in the soil and forms a substantial part of mineral-associated soil organic matter. The association of mineral particles and microbial necromass stimulates the formation of microaggregates inside soil aggregates (Six et al. 2002, 2004). The organic matter bound in soil aggregates, and specially in microaggregates inside aggregates, is more stable and resistant against decomposition (Marín-Spiotta et al. 2008). Despite the remarkable difference in the drilosphere and the surrounding soil, Hedenec et al. (2020) show that the colonization of soil by earthworms leads to significant changes of soil microbial processes not only in drilosphere but also in bulk soil, which was a few cm away from earthworm created structures. This suggests that the effect of earthworms can be much broader than one may have thought.

### *3.2 Bioturbation and Topsoil Formation*

The effect of individual earthworm cast is low, but earthworm cast may accumulate in soil that changes soil condition. Not only by changes that happen inside drilosphere but also the way how individual structures produced by earthworms are moved and organized in soil, in other words by earthworm bioturbation. Bioturbation is a movement of soil by biological processes. In moist soils that do not freeze, earthworms that inhabit that soil can move 10–50 t/ha/y in some tropical locations, rates exceed 100 t/ha/y (e.g., Watanabe and Ruaysoongnern 1984; Krishnamoorthy 1985). Earthworm bioturbation can move soil from deeper soil layers upward but also horizontally in soil. Due to this movement, objects on the soil surface can be buried in the soil, because they are undermined by the earthworm corridor and at the same time covered by earthworm cast, which causes them to sink into the soil. Formation of corridor may affect water movement in soil and root growth (Cheng et al. 2017), which can have implications for soil development. Moreover, bioturbation does not mean only mixing of soil but it also causes the incorporation of organic matter in the soil (Jegou et al. 1998, 2000) and modification of soil properties. Another consequence of simultaneous activities of many earthstorms over time is that certain layers of soil are enriched by earthworm casts that contribute to the formation of soil horizons. Frouz et al. (2007a, 2007b) used thin soil sections to describe how accumulation of earthworm cast corresponds to the formation of the A horizon in the initial stage of soil development in post-mining sites. These results show that, in suitable conditions, almost 10 cm of A horizon can develop in 40 years (Frouz et al. 2009). Most of that layer consists of earthworm casts (Frouz et al. 2009). In addition, soil development in a common garden experiment, where various tree species were planted close to each other on the same post-mining overburden, shows that the increase in A horizon depth is positively correlated with earthworm abundance; furthermore, the A horizon depth and earthworm abundance are negatively correlated with the litter C:N. So, in initial soil development, earthworms strongly affect the formation of the A horizon but are controlled by the litter quality. When C:N ratio is low, such as under alder or lime, almost 10 cm of A horizon can be formed in 40 years, but almost no A layer formation was observed during the same time under spruce and pine with high C:N ratio of litter, despite the fact that these sites were just a few dozen meters apart (Frouz et al. 2013a). Spruce has also low earthworm density, and over time, a thick Oe layer formed by partly decomposed litter accumulated on the soil surface. This clearly shows that earthworms are responsible for litter mixing in soil and fermion of A layer. If earthworms are absent, the litter decomposes on the soil surface without being mixed into the soil. This can be nicely illustrated in unclaimed plots where due to migration constrains and a bit slower development of vegetation lead to slower colonization of sites, by earthworm (Fig. 3). Frouz et al. (2008) show that before earthworms colonize these sites (during the first 15–20 years of soil development), there is no visible formation of A horizon and instead a thick Oe layer of pertly decomposed litter develops on soil surface. When earthworms colonize sites, A layers start to develop.

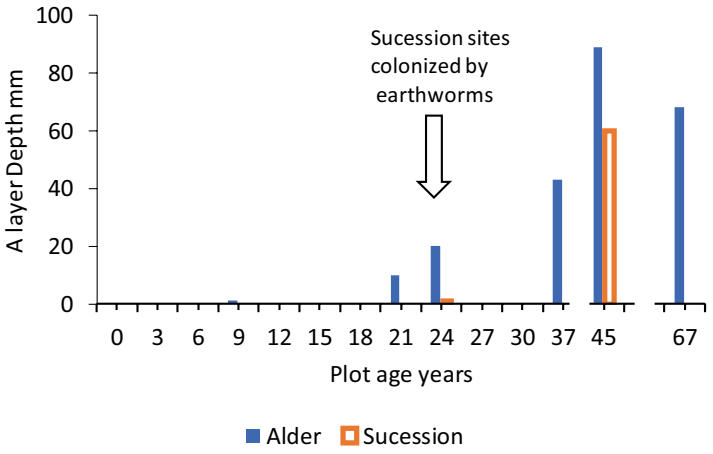


**Fig. 3** Development of the A horizon in post-mining soils near Sokolov (Czech Republic). The alder plantations "Alder" were colonized by earthworms from Year 0 of the study. In contrast, earthworms do not colonize sites with unassisted natural succession "Succession" until 20 years after mining activities cease (based on Frouz et al. 2001, 2008, 2009)

A horizon thickness may reach about 5 cm within 20 years after earthworms colonize the sites. Moreover, the growth of A horizon in these sites is closely correlated to the proportion of earthworm casts in soil volume. All these data strongly support the idea that A horizon formation in the initial stages of soil development may be strongly affected by earthworm bioturbation. However, the formation of A horizon is not linear with time. The growth of A horizon is fast initially and later it slows down (Fig. 3) and eventually stops. This is consistent with the degree of bioturbation decreasing exponentially with time as was mentioned earlier. Studies from post-mining sites (Frouz et al. 2001, 2007a, 2009) show that about 50% of soil volume, or in other words, the majority of solid state of the soil depicted in Fig. 3, is formed by earthworm casts. One may expect that the depth of A horizon corresponds somehow with the depth of bioturbation, not only by earthworms but also by other organisms (Ruiz et al. 2023), but there is little data directly comparing those two.

Formation of A horizon can strongly affect soil development. Soil horizons of young developing soils, where earthworm bioturbation dominates, tend to accumulate carbon (Fig. 4) and have higher microbial biomass and F:B ratio shifted toward bacteria (Frouz et al. 2009, 2013a, 2013b). Shift of fungal-to-bacterial ratio leads to a shift in the whole food web more to bacterial driven (Frouz et al. 2013b). Soil layers that have been largely affected by earthworm activity have greater water retention (Frouz and Kuráž 2014) and also larger porosity and water infiltration (Jačka et al. 2021). These changes in soil condition may yield into changes in plant community composition (Frouz et al. 2008; Mudrák and Frouz 2018), which has been observed during decade after the sites have been colonized by earthworms. Mudrák and Frouz (2018) showed that the changes in plant community arise from the

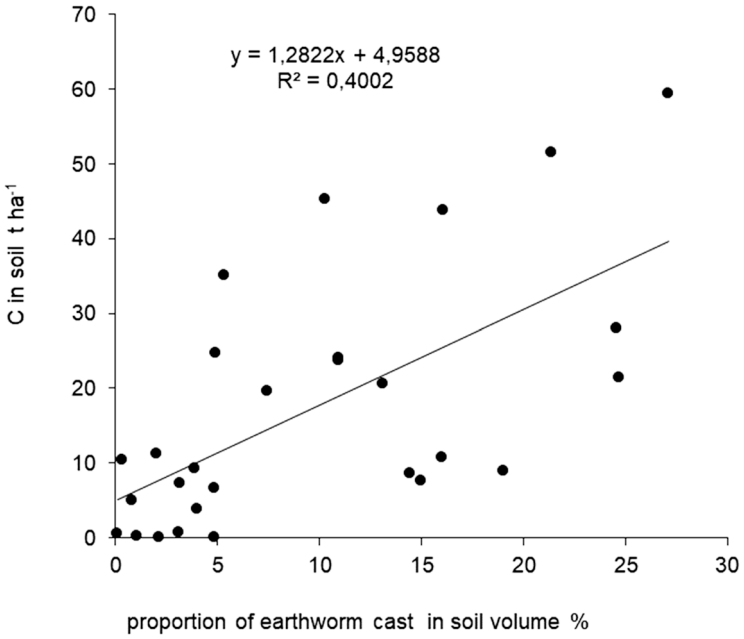


**Fig. 4** Relationships between the earthworm casts in topsoil (0 to X cm) and the soil C concentration in the A horizon developing in post-mining soils near Sokolov (Czech Republic). Based on Frouz et al. (2009), modified

combination of immediate effects fauna had on plants arising, namely, from nutrient availability, but also from long-term changes in soil structure, which develop over a decade or two. In the early stages of development, the effect on soil structure is more pronounced; once soil structure has been established, the immediate effect of earthworms such as effect on nutrient availability becomes more important (Mudrák and Frouz 2018). Earthworms may also change the mycorrhizal association with plants roots. Data from post-mining soils in Czech Republic suggest that earthworms may support arbuscular mycorrhizal fungi preferentially, to the detriment of ectomycorrhizal fungi, which may support changes in vegetation composition mentioned earlier (Frouz et al. 2019). However, it should be highlighted that all these examples come from the initial stages of soil development. With time, the effect of earthworms becomes less pronounced, until it cannot be discerned detected in a developed soil. This is indirectly supported by the observation that in soils that are in the initial stages of soil development (after only a few decades of soil development, such as post-mining heap) growing plants producing litter with low C:N that support earthworm activity support soil carbon storage. The opposite was observed for mature soils where soil development already occurred continuously for several millennia (Hublova and Frouz 2021). More examples on interactions between immediate effects and long-term legacy can be found in Frouz (2024).

### *3.3 Interaction of Bioturbation and Transport Processes from Soil Profile to Landscape*

Bioturbation can also interact with other transport processes, such as clay movement in soil profile, erosion and deposition. Concerning the movement of material in soil profile bioturbation may partly offer eluviation as earthworms are transporting soil from deeper soil including clay particles toward soil surface. In absolute terms, bioturbation brings more clay particles upward than eluviation downward; however, bioturbation intensity strongly non-linearly decreases with depth, which forms an area in deeper layers of soil where eluviation prevails (Sauzet et al. 2023). Bioturbation affects erosion as well. On one hand, as was demonstrated above, earthworms increase infiltration, which may potentially reduce the amount of water moving on the soil surface—and thus the strength of erosion (Jačka et al. 2021; Le Mer et al. 2021). At the same time, cast production may increase soil surface roughness, which may reduce erosion (Jouquet et al. 2008). Other studies show that earthworm casts brought to the surface are more erodible than the rest of the soil and can support water erosion and movement of soil from elevated parts to the slopes downhill where sedimented material can accumulate (Darwin 1881; Román-Sánchez et al. 2019). Still, there is not much data about how earthworms may potentially contribute to mixing this newly sedimented material to existing soil and doing that contribute to increasing A horizon thickness in these areas. However, in areas where large, active earthworm populations exist, they are probably contributing to soil hydrological processes and corresponding intensity of erosion (Bottinelli et al. 2021; Schneider et al. 2018; van Schaik et al. 2014). Along slope catena, bioturbation can thus increase erosion in the upper parts of the catchment. This brings soil-forming substrate closer to the soil surface, which may potentially increase the rate of soil formation. At the same time, eroded material accumulates in the bottom part of the catchment, which can promote the formation of deeper soil there. These processes, happening over large areas, may affect land denudation as already pointed out by Darwin (1881) and more recently confirmed by modern techniques (Johnson et al. 2014; Román-Sánchez et al. 2019). Wilkinson et al. (2009) even postulate that bioturbation-induced soil formation and erosion process can be as rapid as sustained maximum rates of tectonic uplift (Fig. 5).

## 4 Conclusion

Earthworms interact with the key soil-forming factors, at various spatiotemporal scales, which contribute to soil formation. In highly disturbed soils after mining, earthworms are involved with soil formation in the A horizon. Importantly, these earthworm–soil interactions have a nearly instantaneous impact on soil processes such as nutrient release and microbial community structure, which are beneficial for the establishment of vegetation and other biota. While earthworm-mediated

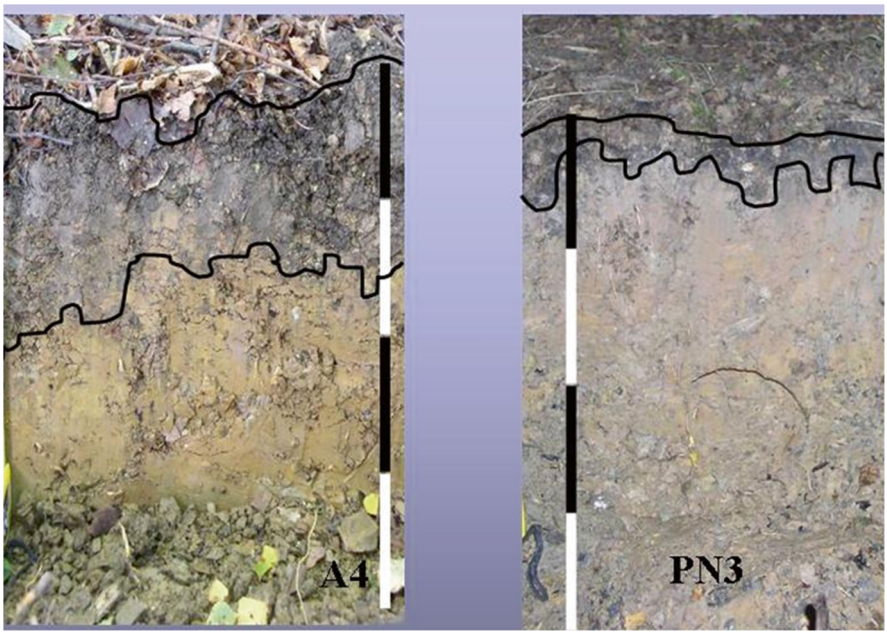


**Fig. 5** Two soil profiles in post-mining soils near Sokolov (Czech Republic). On the left panel is an alder plantation with over 250 earthworms $m^{-2}$, while the right panel is under a pine forest with less than 50 earthworms $m^{-2}$

formation of soil aggregates and preferential flow paths created by their burrowing may have a limited immediate effect, the persistence of these biostructures can become enhanced across space and time. This magnification of an initially small but persistent effect creates a substantial legacy of earthworm engineering that persists even after organisms that started the whole process are already gone.

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